THE DEVELOPMENT OF *LASIOGRAPTUS HARKNESSI* (NICHOLSON 1867)

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ABSTRACT. The development of *Lasiograptus harknessi* (Nicholson) is described, and its significance discussed. A lectotype for the species is proposed. A new monotypic genus, *Dicaulograptus*, is erected with the type species *Lasiograptus hystrix* Bulman 1932.

WITHIN the family Lasiograptidae Lapworth 1879 little is known of the detailed morphology of *Hallograptus* Lapworth, *Neurograptus* Elles and Wood, and *Nymphograptus* Elles and Wood. Of the remaining genera, *Gymnograptus* Bulman and *Lasiograptus* Lapworth, at least fifteen species have been described, but the proximal development is known in only four: *G. linnarssoni* (Moberg), *G. retioloides* (Wiman) (Urbanek 1959 and Jaanusson 1960), *L. hystrix* Bulman 1932, and *L. harknessi* (Nicholson), the development of which is described below.

Each of these four species has a different type of diplograptid development (text-fig. 1). Thus in *G. linnarssoni* (text-fig. 1*a*) th. 1^2 grows directly across and upwards; th. 2^2 is the dicalycal theca, and the rhabdosome is cryptoseptate (Urbanek 1959). *G. retioloides* (text-fig. 1*b*), on the other hand, has th. 1^2 of the 'basic' diplograptid type; th. 2^2 is the dicalycal theca; the origin of th. 2^1 and th. 2^2 is of distinctly primitive appearance, and the rhabdosome is septate. *L. hystrix* has a 'dentatus' stage development, with th. 2^1 the dicalycal theca (text-fig. 1*c*).

The diplograptid development of *L. harknessi*, described herein, further complicates the picture. In this species th. 1^2 grows directly across and downward; th. 2^1 appears to be the dicalycal theca, and the rhabdosome is at first cryptoseptate and finally, beyond the sicular apex, is septate.

Because of the obvious difficulty in assessing the taxonomic rank of the type of proximal development, workers have used thecal form, nature of clathria, and presence of lacinia as a means of classification (Urbanek 1959, Jaanusson 1960, Lee 1963). On this basis Jaanusson considers that the species *L. hystrix* has gymnograptid thecae throughout the length of the rhabdosome; and he doubtfully refers it to the genus *Hallograptus* on the supposition that upon flattening of the rhabdosome *L. hystrix* would acquire a general hallograptid appearance. The placing of *L. hystrix*, even doubtfully, in the genus *Hallograptus* is here considered incorrect. The published figures of hallograptid species, and the specimens examined by the writers in the Sedgwick Museum collections, whilst invariably of flattened material, do seem to have thecae which vary from lasiograptid or gymnograptid proximally, to gymnograptid or orthograptid distally. The thecae of *L. hystrix*, however, are unique in both the degree and nature of the introversion of the apertural margin, and the nature of the thecal spines. Indeed, the thecal form is more reminiscent of the *Dicranograptidae* than the *Lasiograptidae*. It seems to the writers that *hystrix* should be referred to a new, monotypic genus, and the name *Dicaulograptus* gen. nov. is here proposed.

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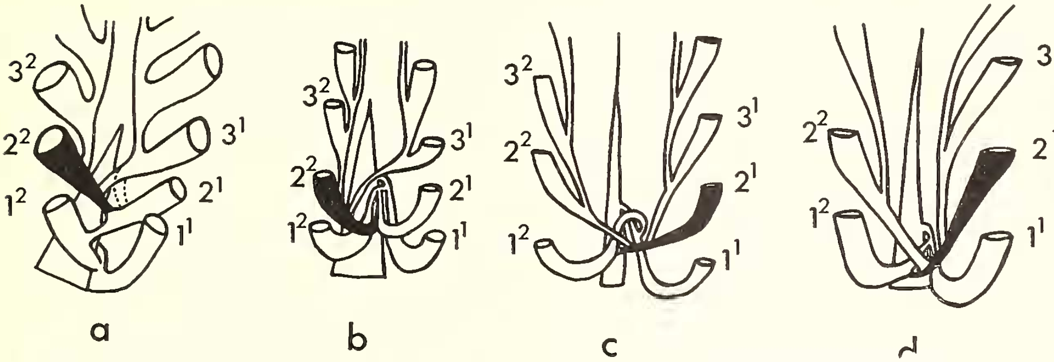
L. harknessi (Nicholson) is therefore the only species, with known proximal development, which can be assigned to the genus *Lasiograptus*.

Material. A single specimen of *L. harknessi* was isolated by Bulman (1947) from the Laggan Burn limestones. This specimen is now deposited in the Geological Survey Museum (no. 74259). The proximal end is opaque and the details of development cannot be ascertained.

At a later date about a dozen specimens were isolated, cleared, and mounted by Miss J. James, and of these, four are well preserved, showing the thecal relationships except at the extreme proximal end. A further specimen, isolated by Miss James, has been



TEXT-FIG. 1. Mode of development of *a*, *Gymnograptus linnarssoni* (after Urbanek 1959); *b*, *G. retioloides* (after Urbanek 1959); *c*, *Dicaulograptus hystrix* (after Bulman 1932); *d*, *L. harknessi*. In each case the dicalycal thecae is shown in black.

cleared and mounted by the writers and this specimen shows the development of the extreme proximal end very clearly.

Specimens of *L. harknessi* from the Laggan Burn section are extremely difficult to mount, owing to a tendency to collapse under their own weight, if the inside of the rhabdosome is not filled with liquid during the whole of the clearing and mounting process. The specimen was therefore transferred in a drop of alcohol to a slide upon which the centre of a large blob of euparal gum had been thinned considerably with euparal essence. The alcohol, and specimen, sank into the euparal. (At this stage, if the euparal is not thinned, the alcohol merely runs off leaving the specimen to collapse.) A thin sliver of blotting paper was then inserted into one of the thecal tubes, and as the alcohol was drawn out of one end of the rhabdosome the euparal entered at the other, thus supporting the rhabdosome continuously. All the alcohol was removed in this manner.

Of the six isolated specimens, five are deposited in the Sedgwick Museum, Cambridge (nos. A54,975–A54,979), and the sixth in the Geological Survey Museum (no. 74259). The lectotype is deposited in the British Museum (Nat. Hist), specimen no. Q53c.

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SYSTEMATIC DESCRIPTION

Order GRAPTOLOIDEA Lapworth 1875
Suborder DIPLOGRAPTINA Lapworth 1880 emend Bulman 1963
Family LASIOGRAPTIDAE Lapworth 1879
Genus LASIOGRAPTUS Lapworth 1873

Lasiograptus harknessi (Nicholson 1867)

Text-figs. 1–3

1867 *Diplograpsus Harknessi* Nicholson, p. 262, pl. 11, figs. 6, 7.
1908 *Lasiograptus* (*Thysanograptus*) *Harknessi* (Nicholson); Elles and Wood, pp. 325–6, pl. 34, figs. 1*a–d*, text-fig. 214.
1947 *Lasiograptus harknessi* (Nicholson); Bulman, pp. 71–72, pl. 8, figs. 11, 12.
1949 *Lasiograptus harknessi* (Nicholson); Sherrard, p. 75, pl. 2, fig. 14, text-fig. 27*a–c*.
1963 *Lasiograptus harknessi* (Nicholson); Geh Mei-yu, pp. 254–5, pl. 5, (?) fig. 17, fig. 18; text-fig. 13*a*.

Lectotype. The specimen figured by Elles and Wood 1908, p. 326, text-fig. 214*b*, and now contained in the British Museum (Nat. Hist.) as specimen no. Q53c.

The counterpart of this specimen was figured as pl. 34, fig. 1*a* by Elles and Wood (op. cit) and was doubtfully referred to the type specimen. Unfortunately the slab from which fig. 1*a* was drawn is now missing. However, the counterpart (Q53) of this slab contains, in addition to Q53c, two proximal ends of *L. harknessi* one of which was figured by Elles and Wood as text-fig. 214*a*. Q53c very closely resembles one of Nicholson's original figures (pl. 11, fig. 6) and it is significant that in his description (p. 262) he records that this slab contained one adult and 'two or three germs'. There can be little doubt that slab Q53 is the counterpart of the slab from which Nicholson drew his description and figures, and from which Elles and Wood figured pl. 34, fig. 1*a*. In view of this the adult specimen (Q53c) is here proposed as lectotype of the species *L. harknessi* (Nicholson).

Material. Six proximal ends in relief; isolated, cleared, or partially cleared, and mounted on glass slides. Numerous specimens, including the lectotype, preserved as flattened films.

Horizon and localities. Corynoides Band, Caradoc Series, Laggan Burn, Ayrshire; Hartfell Shales, Hartfell, Dumfries.

Revised diagnosis. Rhabdosome short; usually 2 mm. or less in width (excluding processes); thecal spacing variable, 10–16 in 10 mm., the highest values being at the proximal end; thecae of lasiograptid type; excavations deep, inclined proximally in dorsal parts of excavation, apertural and pleural lists well developed, parietal lists weak, connecting apertural region to strong aboral lists; development diplograptid, rhabdosome cryptoseptate after th. 2^1 and septate after 3^2; lacinia present (but not preserved in the isolated material); nema prominent, undulating in profile view.

Development. The broad-based sicula is a prominent feature of the proximal part of the rhabdosome. It is exposed on the obverse side for about 1 mm. of its length, and on the reverse side for about one-tenth of a millimetre (text-fig. 3*f*, *g*). The sicular aperture possesses a robust virgella and, opposite this, a pair of equally robust spines. The apex of the sicula lies at the level of the supragenicular wall of th. 3^1.

The prosicula is preserved in two specimens and in the one measurable instance (no. A54,975) is 0·45 mm. in length. No structural details can be ascertained other than a faint longitudinal pattern and a thickening near the apex.

The metasicula is about 1·33 mm. long and widens from 0·13 mm. initially to 0·40 mm. at its aperture. Close to the junction with the prosicula the growth-lines are approximately 0·013 mm. apart, but at the sicular aperture are about 0·03 mm. apart.

Th. 1^1 originates at a point 0·65–0·75 mm. from the base of the sicula, and grows downwards, adpressed to the sicula, for 0·75–0·88 mm. before turning upwards and outwards in a characteristic trumpet shape. There is, of course, no geniculum on th. 1^1 but a single spine arises from a homologous position. The ventral wall above the spine varies from nearly vertical to slightly inclined towards the axis. The apertural margin is almost horizontal in some specimens and undulating in others. In the latter cases the margin is excavated at the dorsal edges of both lateral walls to a depth of up to 0·07 mm. (see text-fig. 2*c*) and two growth-bands may be incompletely developed. On th. 1^1 the growth-lines are initially more closely spaced than on the adjacent part of the sicula, but near the thecal aperture are about 0·03 mm. apart.

The initial bud of th. 1^2 begins to form on th. 1^1 when only 0·08–0·13 mm. of the latter have been laid down, and is not complete until th. 1^1 is 0·3–0·4 mm. long.

Th. 1^2 grows immediately downwards from its broad initial bud and extends almost to the apertural region of the sicula. It begins to turn upwards when it has reached a length of 0·25 mm. and gives rise to a narrow initial bud of th. 2^1 (text-fig. 3*c*). The distal part of th. 1^2 is not dissimilar to that of th. 1^1 in that no geniculum is developed but a spine arises from a homologous position. The ventral wall above the spine is almost vertical and, as in the case of th. 1^1, the apertural region is less undulating than in the more distal thecae. Near the aperture the growth-lines are approximately 0·03 mm. apart.

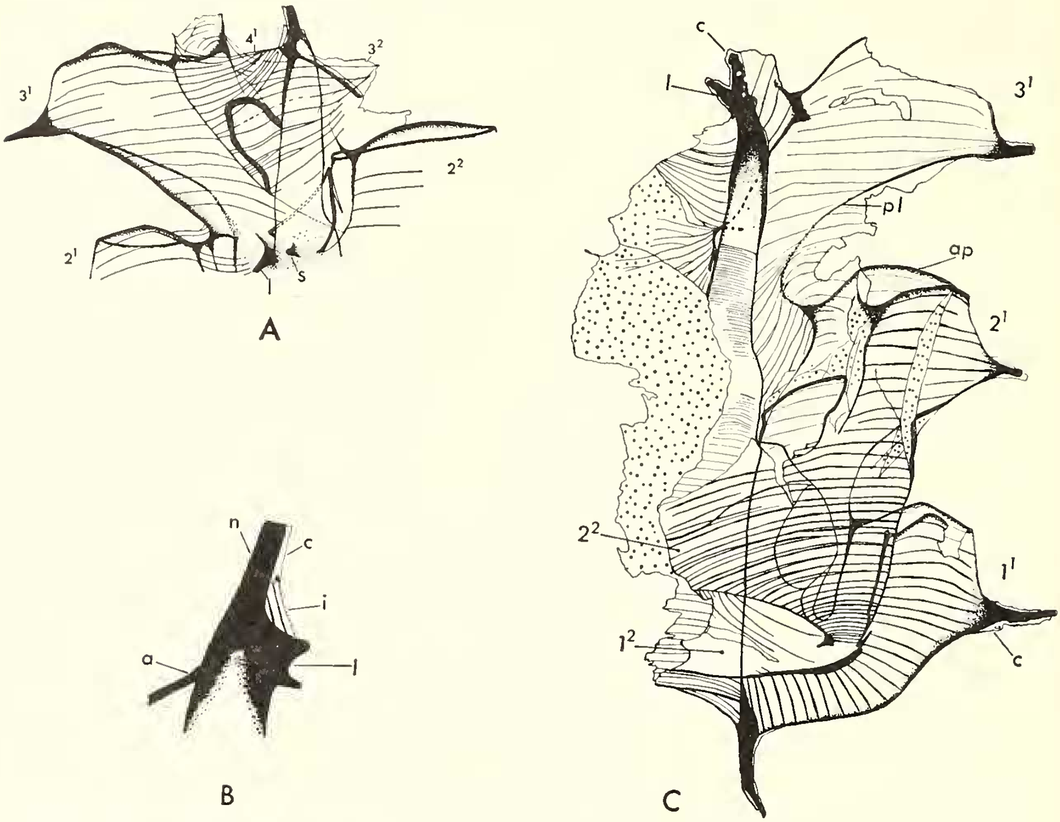
Viewed from the reverse side the bud of th. 2^1 is on the level of the sharp bend in the dorsal wall of th. 1^1 (text-fig. 3*e*), and a transverse spine is positioned on its dorsal side. The separation of th. 2^2 from th. 2^1 is complete after half a millimetre (text-fig. 3*d*).

The thecae beyond th. 1^2 are more typically lasiograptid. The excavations are deep, and in the dorsal region are inclined proximally. The supragenicular wall becomes increasingly inclined towards the axis as successive thecae are developed. Paired spines are developed from the genicula. Successive thecae have similar numbers of growth segments (14–18 on the free ventral wall, 4–6 being in a supragenicular position) but the spacing of the growth-lines increases to about 0·07 mm. at the point where the maximum thecal size is reached (about th. 3^1 or th. 3^2). Thereafter no change can be detected.

Occasionally the proximal extension of the thecal excavation is filled by secondary growth-bands (text-fig. 2*a*) in a manner similar to that described by Urbanek (1959) in the case of *Gymnograptus linnarssoni*.

The apertural and pleural lists are well developed, but the parietal lists are weak. Towards the point where they connect with the apertural lists, the pleural lists become somewhat weaker and in this region the passage of the growth bands across the lists can be seen (text-fig. 2*c*).

The probable origin of th. 2^2 from th. 2^1 has been considered above, but th. 2^1 also possesses a conspicuous foramen flanked by a robust aboral list (text-fig. 2*c*). Th. 2^1 is, on this interpretation, the dicalycal theca and gives rise to both th. 2^2 and th. 3^1. However, there is no trace of a median septum until the apex of the sicula is reached. At the apex of the sicula is a strong transverse rod, and in the angle this makes with the virgula a portion of median septum is preserved (text-fig. 2*b*). The absence of the median septum prior to the sicular apex could be explained as a preservational feature, but this is unlikely in view of the presence of other equally delicate structures, and, indeed, of the median septum itself beyond the sicula.



TEXT-FIG. 2. A, Part of specimen no. S.M. A54,976, obverse view, showing relationships of thecae near sicular apex, ×40 approx. B, Same specimen, portion of median septum preserved between nema and transverse list, reverse view, ×115 approx. C, Simplified camera-lucida drawing of specimen no. S.M. A54,975, reverse view, showing dicalycal nature of th. 2^1, and origins of th. 1^1, 1^2, 2^1, and 2^2; heavy stipple indicates badly preserved areas. ×45 approx. n = nema, c = cortical tissue, i = median septum, l = transverse list, s = spine, a = aboral list, ap = apertural list, pl = pleural list.

If the arrangement of growth-lines on the lateral walls of the rhabdosome is examined (text-figs. 3*f*, *g*) the proximal end might, at first inspection, be deduced as being aseptate

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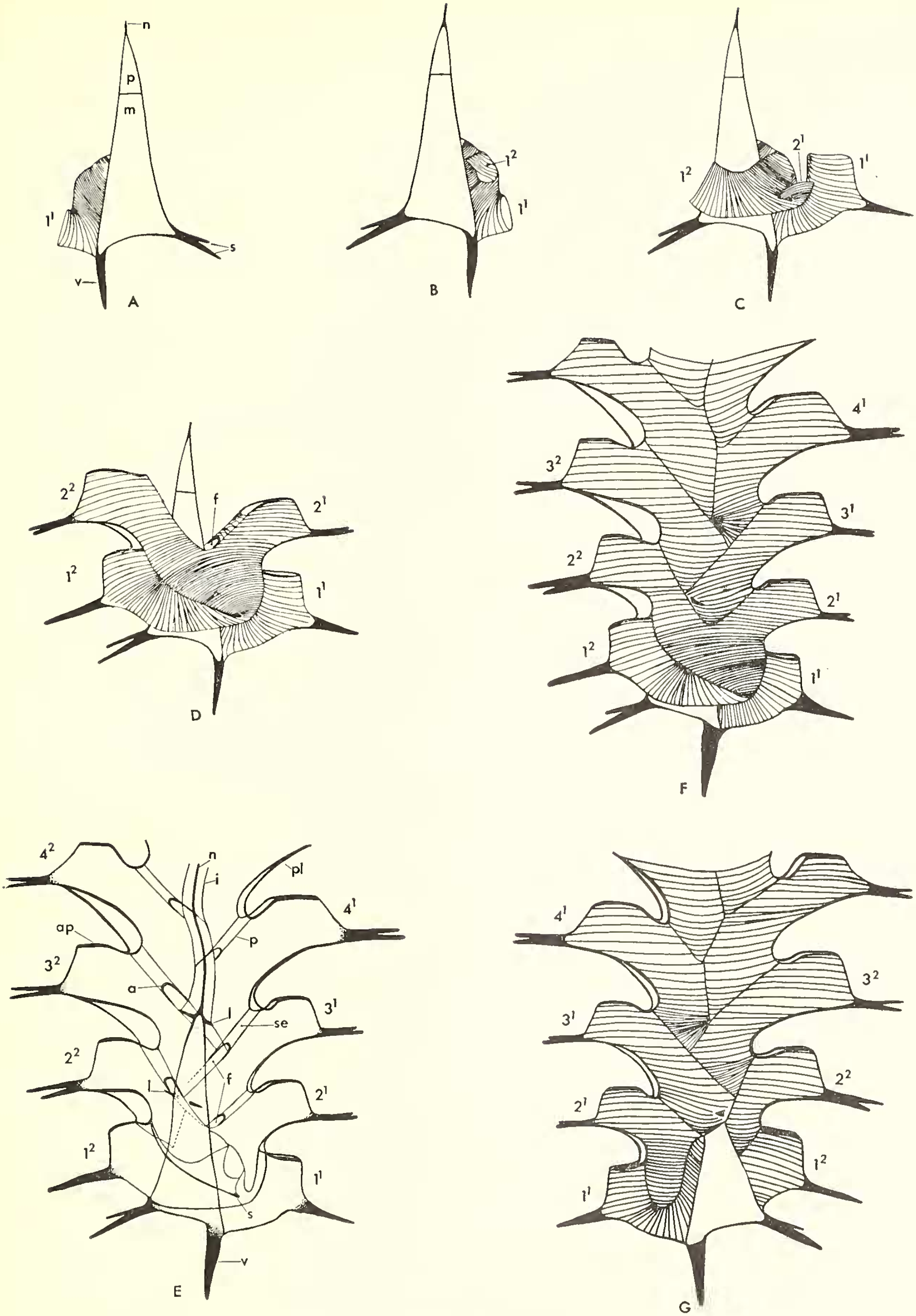
TEXT-FIG. 3. A–D, Development of *L. harknessi*: taken from specimen no. S.M. A54,975. Figures are not growth stages. A, Origin of th. 1^1, obverse view. B, Reverse view showing initial bud of th. 1^2. C, Further development of th. 1^2 and initial bud of th. 2^1. D, Further development of th. 2^1 and origin of th. 2^2. E, Transparent reconstruction of rhabdosome. F–G, Reverse and obverse views respectively, of reconstructed rhabdosome showing growth-lines as they appear on lateral walls. All figures ×25 approx., p = prosicula, m = metasicula, v = virgella, n = nema, i = median septum, l = transverse list, s = spine, a = aboral list, p = parietal list, ap = apertural list, pl = pleural list, f = foramen, se = interthecal septum.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TEXT-FIG. 3.

up to 3^2. But the most proximal growth segments of th. 3^1 appear to be intimately related to th. 2^1 (text-figs. 2*c*, 3*f*, *g*), which implies that two separate series are developed from th. 2^1.

In view of the above evidence it is considered that a cryptoseptate arrangement exists between th. 1^2 and th. 4^1. This interpretation means that the thecae 2^1, 2^2, 3^1, and 3^2 are interconnected.

A puzzling feature which, for preservational reasons, cannot be fully explained, is the presence of transverse rods at certain points on the rhabdosome. These occur at the proximal extremities of the thecal foramina of the second series, and in some cases at least project beyond the lateral walls of the rhabdosome as spines. The first such rod is found about half-way along the sicula near the proximal extremity of the foramen of th. 2^2. It projects from both sides of the sicula (but does not pass through it) and one specimen (S.M. no. A54,976) shows that it extends on the obverse side as a spine. The growth-lines at the proximal end of th. 3^1 appear to be connected with the rod in some way, but the rod itself is so heavily pigmented that the exact relationship remains obscure.

The second transverse rod is at the apex of the sicula, which point coincides with the proximal extremity of the foramen of th. 3^2. The growth-lines at the proximal end of th. 4^1 appear to be directly connected to the rod (text-fig. 2*a*).

Beyond the second rod a true septum is present, but it cannot be ascertained whether any further rods exist. It is not impossible that the rods described are in fact homologous with septal lists.

Remarks. The Laggan Burn specimens described above are assigned to Nicholson's species *L. harknessi* mainly on the grounds of rhabdosomal width. Thus whilst our largest specimen (Geol. Surv. no. 74259) is of similar width at the level of th. 4 to the type specimen of Lapworth's species *L. costatus*, it is thereafter parallel-sided and at the level of th. $5^2/6^1$ is only 1·5 mm. wide. There is no indication of any greater widening distally.

INCERTAE SEDIS

Genus DICAULOGRAPTUS gen. nov.

Type species. *Lasiograptus hystrix* Bulman 1932.

Diagnosis. Rhabdosome minute, slender, slightly less than 1 mm. wide at origin, 1·1 mm. wide at level of second pair of thecae and thereafter parallel-sided. Thecae about 20 in 10 mm., scarcely overlapping, provided with long mesial spines. Th. 1^1 and th. 1^2 provided with pair of slender lateral spines in region of aperture; succeeding thecae with pair of slender lateral spines at proximal end of free ventral wall. Apertural margin of all thecae strongly introverted; in th. 2^1 and later thecae the introverted lip becomes fused with lateral portion of apertural margin resulting in a pair of lateral foramina.

Derivation of name. *caula*, L. opening, hole.

CONCLUSIONS

It is clear from the above that each of the four species, in which the proximal development is known, has a different mode of diplograptid development. Until more species are known in comparable detail the mode of development cannot shed much light on the classificatory or evolutionary problems within the Lasiograptidae. Thecal form remains the only basis for classification; that it may also be a guide to evolution has been suggested by Urbanek (1959, pp. 327–9).

Urbanek considers that *Lasiograptus* may have developed from an ancestor with amplexograptid thecae and, like Jaanusson (1960, p. 335), implies that *Lasiograptus* has uniform thecae. That this is not the case with *L. harknessi* has been demonstrated above. The presence of 'angular fuselli' in *harknessi* also places in doubtful standing another of Urbanek's distinctions between *Gymnograptus* and *Lasiograptus*. The main distinctions between the two genera would seem to be the length and inclination of the supragenicular wall, the presence or absence of a zigzag list on the lateral walls of the rhabdosome, and, to a lesser extent, the nature of the excavation.

The presence or absence of a lacinia is of more doubtful value in taxonomy, if only for the reason that it is rarely preserved, and it is here considered that the erection of the genus *Prolasiograptus* by Lee (1963), for those early *Lasiograptus* species apparently lacking lacinia, is impractical.

The recognition of a cryptoseptate development, in part, for *L. harknessi*, is in accordance with the work of Urbanek and Jaanusson, and it is perhaps to be expected in genera in which the periderm is being reduced. A further point of significance is that in those species in which the internal structure is not known, but in which the growth-lines of the lateral rhabdosomal walls suggest an aseptate development, the presence of an early dicalycal theca, and hence two series, may be obscured. Finally, in those species having a partial median septum, rhabdosomal control may still be effected by an early dicalycal theca. It is not impossible that a species may have a septate development on one side of the rhabdosome, and a cryptoseptate development on the other. On the cryptoseptate side of the rhabdosome the growth-lines might suggest an aseptate arrangement of thecae.

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